NONINVASIVE GENETIC SAMPLING WITH A BAYESIAN SPATIAL CAPTURE-RECAPTURE ANALYSIS TO ESTIMATE ABUNDANCE OF ROOSEVELT ELK (*CERVUS CANADENSIS ROOSEVELTI*)

By

Makenzie Henk

A Thesis Presented to

The Faculty of Humboldt State University

In Partial Fulfillment of the Requirements for the Degree

Master of Science in Natural Resources: Wildlife

Committee Membership

Dr. Micaela Szykman Gunther, Committee Chair

Dr. Daniel Barton, Committee Member

Dr. William Bean, Committee Member

Ms. Carrington Hilson, Committee Member

Dr. Erin Kelly, Graduate Coordinator

May 2021

ABSTRACT

NONINVASIVE GENETIC SAMPLING WITH A BAYESIAN SPATIAL CAPTURE-RECAPTURE ANALYSIS TO ESTIMATE ABUNDANCE OF ROOSEVELT ELK (*CERVUS CANADENSIS ROOSEVELTI*)

Makenzie Henk

Determining abundance of Roosevelt elk (*Cervus canadensis roosevelti*) in central Humboldt County, California has presented a unique challenge to wildlife managers due to the dense forest habitat and the animals' elusive behavior. As the elk population has increased, so has human-wildlife conflict, and wildlife agencies need efficient and repeatable methods for determining abundance to inform management decisions. Traditional monitoring methods such as helicopter surveys are ineffective due to low sighting probability and strong behavioral responses to the aircraft. They also often lead to biased sex ratios when the distribution of males and females varies across the landscape. Non-invasive genetic sampling combined with spatial capture-recapture (SCR) is an alternative approach to monitoring populations that are difficult to observe directly. This study combined a Bayesian SCR with a binomial point process modeling approach and an unstructured single survey search method to estimate elk abundance. We aimed to increase the count of males by using a detection dog to search forested areas, and searched open grassy hillsides for cow-calf groups. Additionally, GPS collar data were used to quantify cohesion of movement among elk through a spatiotemporal analysis of home ranges. Over two seasons, we genotyped 436 unique individuals (326

females, 110 males). For the SCR analysis, we used sex and survey effort as covariates in detection probability, and used a "trap"-level random effect to account for the overdispersion in the count data from the herding behavior of elk. The population estimate in the study area was 618 ± 36.34 individuals (95% BCI 551-693) with a density of 1.09 ± 0.06 elk per km^2. This study demonstrated a reliable way to obtain a biological reasonable population estimate for elk in an area that is not conducive to traditional monitoring methods.

ACKNOWLEDGMENTS

This research was made possible through a collaboration between the California Department of Fish and Wildlife (CDFW) and Humboldt State University. I am deeply grateful for the funding and resources provided by CDFW through the federal Pittman Robertson grant and the Big Game Management Account grant to conduct this research.

First, I would like to thank my advisor, Dr. Micaela Szykman Gunther, for all the support and guidance as I navigated through graduate school and the research process. Likewise, I am very grateful and thankful for all the help and support from Carrington Hilson, who everyday makes the elk project a success through her tireless efforts and dedication. I would also like to thank the other members of my graduate committee, Drs. Tim Bean and Daniel Barton. The guidance you both provided on my study design and analysis was invaluable.

I would like to thank the previous graduate students; Rudy Mena, Adam Mohr and Erin Zulliger, whose work on the coastal elk population made this project possible by providing information on survival, habitat use and sampling recommendations.

Additionally, I would also like to acknowledge and thank Marlen Richmond for providing the detection dog services, as well as Erica Tevini and Andrea Widjaja for being the best field crew one could ask for. A big thank you goes out to all the undergraduate volunteers that make so much of the elk project possible. Likewise, this research required the cooperation from numerous private landowners and the Green

Diamond Resource Company. I would like to thank you all for allowing myself and the research team access to your property to conduct our surveys.

Last but not least, I would like to thank Dr. Benjamin Sacks and his lab team from the University of California-Davis Mammalian Ecology and Conservation Unit of the Veterinary Genetics Laboratory for conducting the genetic analyses on elk fecal samples and whose research on the genetics of elk made this project possible.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Effective management of recovering species is dependent on an understanding of their population dynamics and distribution. Many stakeholders such as wildlife managers, conservationists, and private land owners, rely on accurate population estimates to make fundamental management decisions on hunting and fishing quotas, land use practices, and to mitigate human-wildlife conflict (Gibbs 2000, Goode et al. 2014). Therefore, it is necessary for managers to devise efficient and repeatable methods for monitoring recovering species (Reed et al. 2011). However, this can be challenging for elusive and wide-ranging species that occupy habitats that are difficult to reach due to steep topography, dense vegetation, or restricted access.

Ungulate populations are frequently of great interest to a broad range of stakeholders because they are popular for wildlife viewing, hunting tags can bring in revenue for natural resource departments, and ungulates can be a source of human-wildlife conflict through property damage and vehicle collisions (Donovan and Champ 2009, Goode et al. 2014). Many ungulate species such as elk (*Cervus* sp.) and deer (*Odocoileus* sp.) present a unique challenge for population monitoring because individuals are rarely uniquely identifiable and can have large home ranges. Aerial surveys have been the primary method of obtaining spatially robust count data for wide-ranging ungulates (Lubow and Ransom 2016). However, these data can be biased even after being corrected with a sightability model if sighting probability was low or the helicopter/aircraft provoked a strong behavioral response (Lubow and Ransom 2016).

Further, bias in estimated sex ratios can occur when the distribution of males and females varies across the landscape (McCorquodale 2001). For instance, in most elk populations, a proportion of males live primarily alone or in small bachelor herds and are rarely available for visual detection. Movement data from telemetered males may be necessary to correct such biased estimates for sex differences in detection probability (Griffin et al. 2013). Bias in aerial survey data is especially common for populations that are difficult to observe directly due to dense forest that easily provides cover when individuals are spooked.

Camera traps are an emerging alternative for estimating abundance of more elusive populations of ungulates, but many analyses that do not require individual identification such as Random-Encounter Models (REM) and Time-to-Event Models (TTE) require auxiliary information on movement rate (Rowcliffe et al. 2008, Moeller et al. 2018). This necessitates capturing and collaring a sufficient number of individuals to obtain movement data that can be generalized to the entire population. This process can be time and resource intensive and reduces the non-invasive aspect of camera trapping preferred by many wildlife professionals. N-mixture models from camera data are another method for inferring abundance from count data. However, their reliability has been called into question under field conditions where probability of detection cannot be fully explained by covariates, and when closure cannot be assumed from sampling occasion to occasion (Barker et al. 2017).

Recently non-invasive genetic sampling methods have been increasingly used for studying ungulate populations (Harris et al. 2010, Poole et al. 2011, Lounsberry et al.

2015, Woodruff et al. 2016). Individual genotypes derived through DNA microsatellite analysis from scat or hair can provide reliable information on individual identity, sex, and relatedness, which are valuable demographic parameters (Palsbøll et al. 1997, Kohn et al. 1999, Woods et al. 1999, Lukacs and Burnham 2005). Non-invasive genetic sampling is a useful tool to generate spatial encounter data for spatial capture-recapture (SCR) modeling. This approach builds on traditional capture-recapture (CR) data by linking the encounter data with the location of the detections through a spatial point process as well as to describe realized density in the model state-space (Royle et al. 2013). This process allows researchers to better estimate the effective sampling area, a problem that plagues CR studies where the estimated population size is not associated with a particular area (Royle et al. 2013). The SCR approach can also increase sampling efficiency by allowing for recaptures to occur either across time or across space in a single survey method (Royle et al. 2013).

Many ungulate species are not exclusively solitary and do not move fully independently of each other, which violates assumptions of the homogeneous binomial or Poisson point process (Royle et al. 2013). Sampling these species that cluster or have dependent movements, i.e., cohesion, can lead to overdispersed count data where the variance in number of individuals captured per trap is larger than the expected variance (Bischof et al. 2020). Previous simulation studies have found that SCR abundance estimates are robust to the violation of model assumptions caused by low levels of grouping and cohesion. However, even in simulated populations with groups of only eight individuals, such as wolf (*Canis lupus*) packs, SCR based on the Poisson point

processes can yield biased abundance estimates (López-Bao et al. 2018, Bischof et al. 2020). These simulations assumed that all groups were the same size with the same level of cohesion, which may not capture the heterogeneity of herding behavior in elk, and the impact that behavior ultimately has on SCR population estimates.

This study used non-invasive genetic sampling with fecal DNA to conduct a single survey SCR analysis on Roosevelt elk (*Cervus canadensis roosevelti*) in central Humboldt County, California. Roosevelt elk populations in California were decimated in the late 1800s, but the population size has been increasing along the North coast since the 1970s (CDFW 2018). The coastal elk population has recently expanded into central Humboldt County and has been increasing in size over the last decade (CDFW, unpublished data). However, population monitoring has been difficult in this area due to steep terrain and restricted access. As human-elk conflict has increased, management agencies aim to better estimate elk population numbers to increase hunting opportunities while also maintaining a healthy population (CDFW 2018). Elk in this area form groups of varying sizes from small bachelor groups of a few all-male individuals to larger primarily cow-calf groups of 100 or more (CDFW, unpublished data). Cohesion of movement among elk can vary by individuals, group, and throughout the year, but is generally highest during the winter months (Franklin et al. 1975). This study attempted to measure the levels of cohesion among elk through a spatiotemporal analysis of collar data and to limit the impact of overdispersion caused by social grouping behavior on the SCR model's abundance estimate. The overall objectives of this study were 1) to provide a precise abundance estimate for the elk population in central Humboldt County; 2) to

evaluate a potentially reliable and repeatable method of estimating elk abundance in dense forest and open grassy habitats; 3) to increase the count of males through an unstructured search method that targets those habitat types.

METHODS

Study Area

The study area was located in the Northern Coastal Mountains of central Humboldt County, California (Figure 1). Humboldt County has a maritime climate characterized by cool wet winters and warm dry summers with annual rainfall averaging between 178 and 205 cm (Sugihara et al. 1987). Snow-fall in the winter is common at the higher elevations, but rarely persists on the ground all season (Kolbe and Weckerly 2015). The study area was approximately 329 km^2 bordered by Hwy 299 to the north and the Mad River along the west and south. The topography ranges from around 60 to 1200 m and is composed of steep grassy hillsides and dense forest (Google Earth 2018). The landscape is a patchwork of private land managed primarily for timber, followed by private cattle ranches and scattered farms. The vegetation is a mix of fir forests (*Pseudotsuga menziesii*) and annual grassland/pasture, with scattered pine (*Pinus* sp.) and redwood (*Sequoia sempervirens*) forest (Humboldt County 2002).

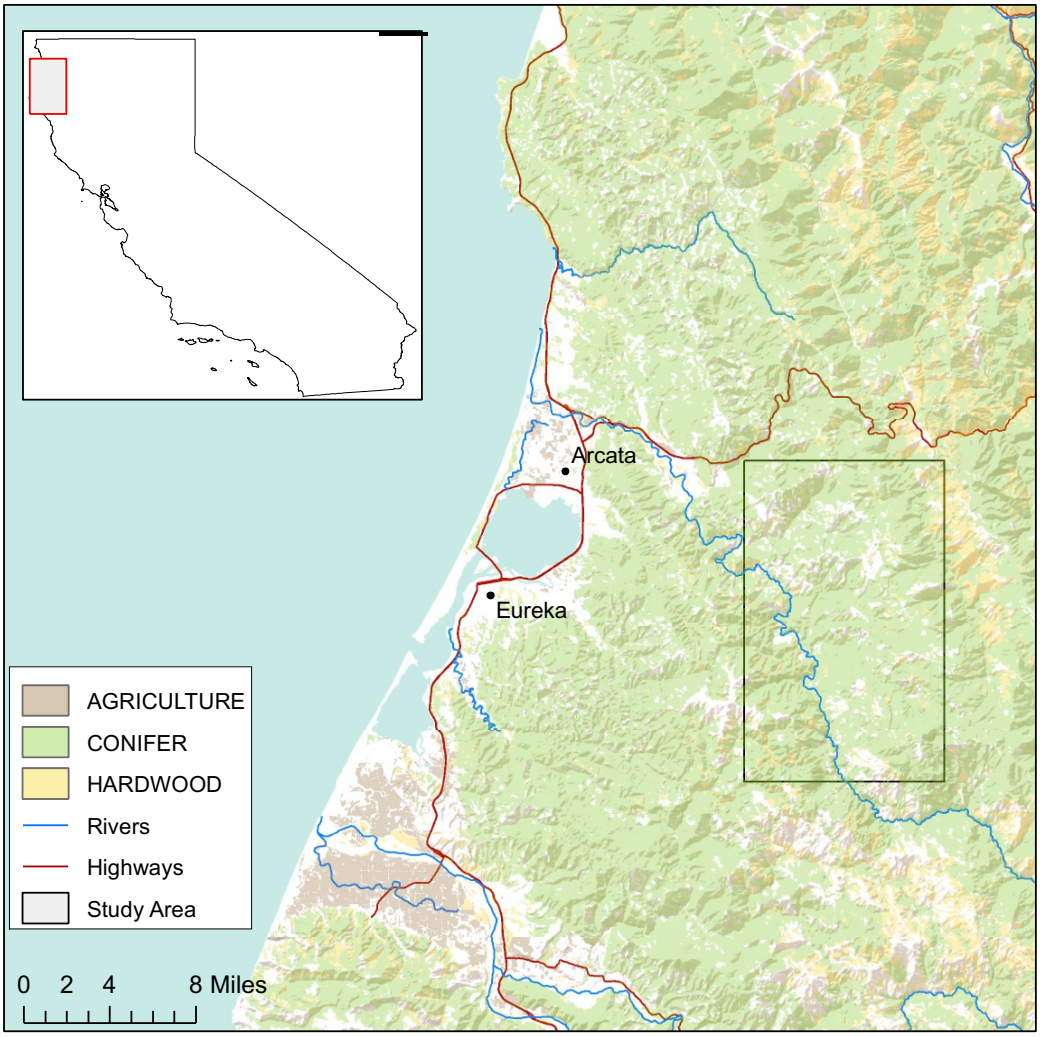

Figure 1. Study area for the fecal DNA collection of Roosevelt elk (*C. c. roosevelti*) during January through March of 2019 and January and February of 2020 in Humboldt County, California, USA.

2019 Fecal Collection

A preliminary field season took place from 4 January to 13 March, 2019. The mid-winter season was chosen to avoid the influx of males during rut in the late summer and fall and the dispersal of females for parturition in the spring and early summer. All collection methods described below were approved by Humboldt State University's Institutional Animal Care and Use Committee (Protocol # 18/19.W.65-E).

During the 2019 field season, myself and a group of volunteers sampled from 4 collared elk groups which each had 1 to 2 collared cows. Cow elk were captured between 2018 and 2019 by the California Department of Fish and Wildlife using free range darting and chemical immobilization with 2 ml of BAM (27.3 mg of butorphanol tartrate, 9.1 mg azaperone tartarte and 10.9 mg medetomidine HCL) and then fitted with a GPS collar (CDFW, unpublished data). The elk groups with collared cows were sampled 1-4 times by 2-4 surveyors on days without rain and minimal rain the day before. We used recent GPS collar points to determine locations to search for fresh fecal pellets (0-6 days old), characterized by being moist with a mucus sheen, and odorous with limited decomposition by insects (Weckerly et al. 2004). We collected 6 pellets from each pellet group with a pair of fresh nitrile gloves and stored them in 50 ml conical tubes (Goode et al. 2014). To avoid sampling from >1 individual per vial, we defined a group of pellets as >10 pellets within 0.1 m^2 from each other (Harris et al. 2010, Månsson et al. 2011). We also collected from the center of each pile, and each pellet group was destroyed and covered with leaf litter, grass or dirt to prevent resampling. Upon returning from the field

the tubes were filled with 95% ethanol for DNA preservation (Lounsberry et al. 2015). These data were not used for the subsequent SCR analysis but were combined with the 2020 genotypes to determine a minimum population count.

2020 Fecal Collection

The 2020 field season was conducted from 6 January to 29 February. We chose surveying locations from a grid of 9 km^2 cells transposed over the study area. The cell size was chosen because it was small compared to the average home range size (32.13 km^2) estimated from 7 collared elk, but provided sufficient search area and habitat variability. Cells were categorized based on habitat suitability and property access (see Appendix for details). Previous work on habitat suitability for female elk determined forest edge and grassland were highly suitable habitat, with tracts of continuous forest classified as lower suitability (Mohr 2020). Further, since male elk can differ in their spatial and temporal use of habitat, we prioritized cells with a mix of habitat types to target both cow-calf groups and male bachelor groups (Weckerly et al. 2004, Bliss and Weckerly 2016). The cells were surveyed in random order except when property access was limited to a short period of time.

Each cell was searched via 2 simultaneous surveys. A detection dog team (dog and handler) searched forest and edge habitat, and a separate team composed of a researcher (self) and technician searched the open grassy hillsides. Both surveys were structured by a path predetermined using Google Earth to control for spatial coverage,

length and elevation gain. The path was adjusted in the field depending on time, terrain, and fecal pellet locations. The same dog and handler were used for each survey to reduce bias (Dahlgren et al. 2012). The starting location for each survey depended on ease of access; as a result, some surveys started outside the cell. Likewise, the routes searched would stray outside the cell if there was not sufficient forest or grassland accessible for surveying from the starting point. Each surveyor and the detection dog had a GPS tracker to measure search effort, and we collected GPS waypoints for all fecal piles from which samples were collected. Collection and storage were conducted using the same protocol as in 2019.

Genetic Analysis

Fecal pellets were processed for microsatellite markers to determine individual identity and sex at the University of California, Davis Mammalian Ecology and Conservation Unit of the Veterinary Genetics Laboratory using a process described in Lounsberry et al (2015). Briefly, epithelial cells were washed from the surface of the fecal pellets using an ATL (Qiagen) buffer. The DNA was then extracted from the resulting solution of suspended epithelial cells, and the microsatellite markers were amplified using a Qiagen multiplex polymerase chain reaction (PCR) kit (Lounsberry et al. 2015). Twelve microsatellite and a sex marker developed for Tule elk (*Cervus canadensis nannodes*) were used for individual genetic profiles and sex determination (Sacks et al. 2016). The DNA-determined individual identities were used in subsequent

analyses if at least 11 out of 12 microsatellites plus the sex marker successfully amplified.

Spatial Capture-Recapture Analysis

We estimated elk population size within the buffered study area using a spatial capture-recapture modeling approach with a homogenous binomial point process. We modeled the baseline encounter probability, p_{0ij}, using a linear mixed effects function which included a covariate, sex, for each individual *i* and a spatial covariate, effort, for each cell *j* with β_1 and β_2 as the parameters to be estimated. We defined effort as the linear distance searched in each cell in kilometers. Further, the baseline encounter probability at cell *j* was treated as a normally distributed random variable to reflect differences in detection probability among cells unmodeled by the other covariates:

$$p_{0ij} = \alpha_j + \beta_1 * Sex_i + \beta_2 * Effort_j$$

The spatial component of SCR allows the model to simultaneously estimate population size along with home range centers, also referred to as the individual's activity center, as a latent variable (Royle et al. 2013). This modeling approach allowed for a heterogeneous probability of detection that decreased as the distance between the location of the individual's latent activity center and the 'trap' location increased. The decline in probability of detection with increasing distance from an individual's activity center was measured as a scale detection parameter (σ), which was related to the estimated home range size (Royle et al. 2013). For this analysis, the spatial component contained σ and

d_{ij}, the distance between the latent activity centers and the traps, in a logistic link function with the baseline encounter probability:

$$logit(p_{ij}) = p_{0ij} - \left(\frac{1}{2\sigma^2}\right) d_{ij}^2$$

We used an unstructured search method with only a single survey per location; no physical traps were used. Instead, traps were defined as the centroid of each grid cell. Genotyped individuals were assigned to the trap(s) for the cell(s) they were sampled in, and could be assigned to multiple traps if they were found in multiple grid cells. However, individuals could not be counted more than once per cell, and thus only be 'caught' once per 'trap' (Royle et al. 2013). As it was not possible to accurately age genotyped fecal pellets, the search occasions were collapsed into a single occasion represented with a bi-dimensional matrix (i x j). Therefore, the probability of detecting individual i in cell j, p_{ij}, was defined by a binomial distribution:

$$y_{ij} \sim binomial(p_{ij})$$

We used grid sizes of 1 km^2, 4 km^2, and 9 km^2 to test the effect of spatial resolution on σ. The study area was buffered by 4.5 km using the 'zeros trick', because grid cells were distributed in a non-rectangular array (R.B. Chandler, pers. comm.). This buffer size was slightly larger than twice the estimate for the scale detection parameter, and therefore reduced the probability of detecting an elk with an activity center outside the state space to near zero (Royle et al. 2013). We also ran a model with a buffer of 10 km to test the sensitivity of the density estimate and the estimates for the baseline encounter probability covariates, sex and effort, on the size of the state space. We

conducted all analyses using the package jagsUI v1.5.1 in R (Kellner 2019, R Core Team 2020).

We used parameter-expanded data augmentation to estimate the number of individuals that were not captured by adding 461 all-zero capture histories (for a total of 750 possible individuals) to the capture history matrix, and modeling the probability an unobserved encounter history was included in the population as the parameter Ψ (Royle et al. 2013). This amount of augmentation was large enough that the distribution of the posterior density estimate was not truncated or limited by the number of individuals (Royle et al. 2013). We used minimally informative priors for all model parameters. The priors used for β_1 and β_2 were normal(0, 0.01), and gamma(0.001, 0.001) for σ. The prior for the random effect was normal(mu, tau) with mu defined as normal(0, 0.01) and tau as uniform(0,10). Models were run for 50,000 iterations with a burn-in period of 25,000. Markov Chain Monte Carlo (MCMC) convergence was assessed through the *R-hat* statistic and visual inspection of the plots. *R-hat* values less than 1.1 were accepted as indicating convergence (Gelman et al. 2014). We assessed goodness of fit by evaluating 2 fit statistics from Royle et al. (2013) using the Bayesian *P*-value approach. Briefly, the first fit statistic tests individual encounter frequencies, and the second fit statistic tests trap-encounter frequency. A Bayesian *P*-value near 0.50 indicated a good model fit.

Cohesion and Home Range Analysis

We attempted to quantify cohesion through a spatiotemporal comparison of GPS collar data for pairs of collared elk whose home ranges overlapped and were believed to belong to the same group. To do this, we created a minimum convex polygon (MCP) for every point taken within a 24-hour period during January and February of 2019 and 2020 for each of the 6 collared elk using the R package adehabitatHR v 0.4.18 (Calenge 2006). The collars were set to take points every 4 hours, so each MCP included up to 6 points. Any 24-hour periods with fewer than 3 points could not be turned into MCPs and were not used for the analysis. We calculated the percent overlap of the MCPs in the same 24-hour period for each of the 3 pairs of elk, which was used as a proxy for how cohesive or dependent the pairs' movements were. For simplicity and ease of comparison, elk pairs were considered to have high cohesion when the MCPs overlapped >75%, medium cohesion when overlap was between >25-75%, and low cohesion when overlap $\leq$25%. We also created 25% and 50% KDE home ranges for these elk to represent 'core' areas of use; these were compared for overlap and compared to the density map of latent activity centers.

Additionally, we created home ranges using a 95% kernel density estimate (KDE) with plug-in method for the 6 collared elk used in the cohesion analysis plus an additional elk collared in the study area. These home ranges were made using points overlapping the study period (January and February 2020) and points between February 2019 to February 2020 for a yearly home range (Walter et al. 2011, Walter and Fischer 2016). We

compared these to the home range estimate derived from the SCR model using σ and the mean baseline probability of detection in the hra function from Royle et al. (2013) adjusted to include the logistic distribution.

The collar data were also used to make a rough approximation of σ by calculating the standard deviation of the coordinates for each collared elk, then taking the mean of the standard deviations weighted by the number of points for each elk. This was done using only the points overlapping the study period ($\hat{\sigma}_{hr}$) as well as the full year of points ($\hat{\sigma}_{hr2}$).

RESULTS

Fecal Collection and Genotyping

We surveyed for fecal pellets on 13 days across 30 cells. The minimum amount of survey effort in a cell was a search track of 8.6 km; however, all other cells had at least 10 km of survey effort with a mean of 29.6 km (Figure 2). We collected a total of 886 samples in 2019 and 1020 samples in 2020. The success rate of the microsatellite genotyping was 95% (n = 841) in 2019 and 78.3% (n = 798) in 2020. The fecal DNA analysis genotyped 230 individuals (197 females, 33 males; 100 females:17 males) in 2019 and 289 individuals (202 females, 87 males; 100 females:43 males) in 2020. There was a significant proportion of males genotyped in 2020 compared to 2019 ($X^2_{1,519}$=17.887, p<0.001). Of the 2020 individuals, 18 males and 7 females were only 'captured' by the detection dog, which increased the number of males detected by 20%.

Eighty-three individuals (73 females, 10 males; 36% of 2019 individuals, 29% of 2020 individuals) were caught both years, giving a minimum count of 436 elk (326 females, 110 males; 100 females:34 males) summed over the 2 sample years. We believe this was an appropriate estimate for minimum count because visual counts in this area suggested a growing population and the mild climate led to high survival rates among yearlings and adults (Nigon 2020, CDFW, unpublished data).

The sex ratios above were adjusted to remove calves by using calf:cow ratios obtained from visual counts of collared elk herds across Humboldt County. These counts were obtained from December 2020 through February 2021 when a concerted effort was

made to obtain accurate calf:cow ratios. The average ratio from these visual counts was 28 calves:100 cows. Assuming a 50:50 sex ratio for calves, there was an average of 14 male and 14 female calves for every 100 cows. After we subtracted the proportional number of calves from the 2020 genotypes, the remaining counts were 174 females and 59 males for a sex ratio of 100 females:34 males. The new sex ratios for the 2019 individuals and the combined 2019 and 2020 individuals were 100 females:3 males and 100 females:23 males, respectively. The resulting 2020 and combined 2019-2020 estimated sex ratios were still above the average ratio (100 females:19 males) from the visual observation counts and the 2020 ratio was larger than the highest sex ratio obtained for any herd through visual counts conducted during that season (100 females: 33 males).

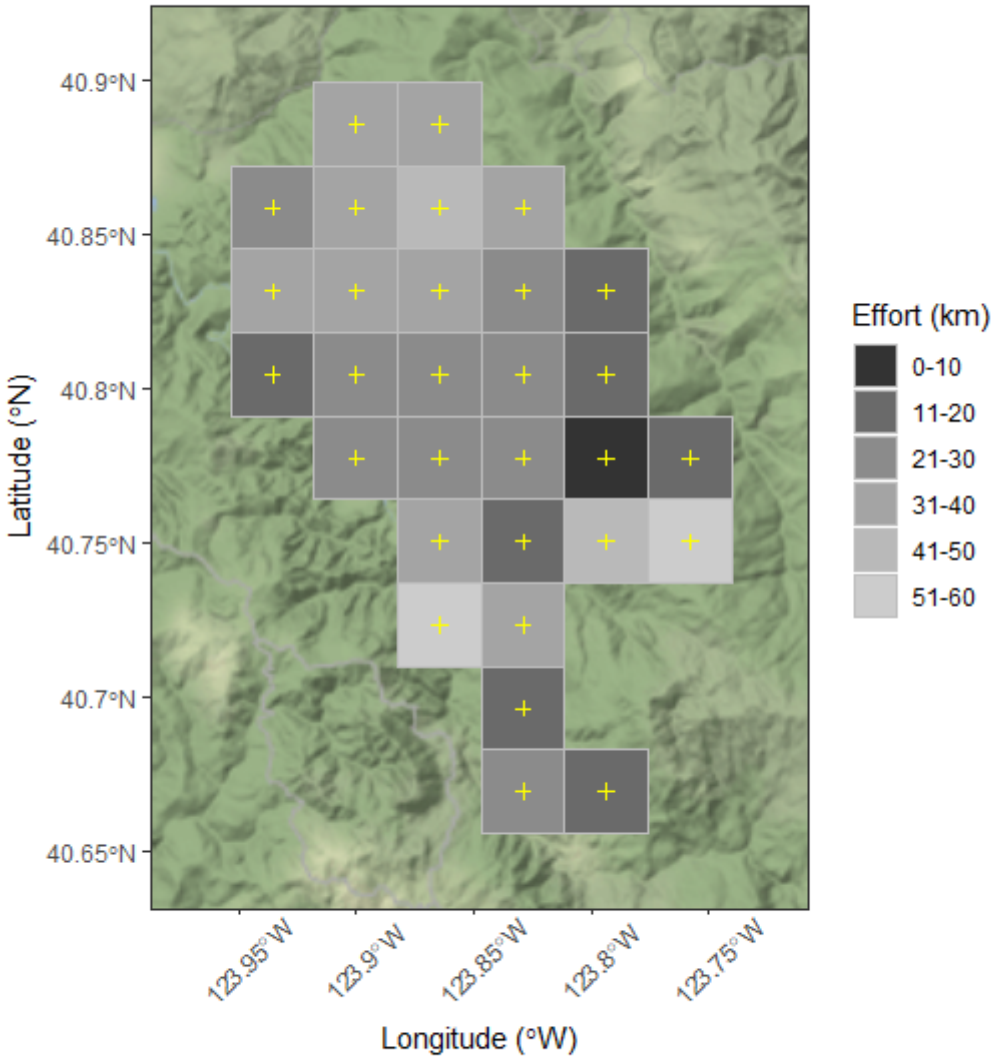

Figure 2. Map of area surveyed in January and February 2020 for Roosevelt elk (*C. c. roosevelti*) in Humboldt County, California, USA. The 9 km^2 grid is shown with spatial 'traps' represented by yellow "+", and each cell is colored based on intensity of search effort in km walked.

Spatial Capture-Recapture

From the 2020 SCR analysis, the average number of spatial captures for the 9 km^2 grid per individual was 1.64 (females = 1.67, males = 1.56), with 154 individuals captured once, and 94, 33 and 8 individuals caught 2, 3, and 4 times for a total of 473 captures (Figure 3). The mean of the posterior probability distribution of abundance from the SCR model was 618 ± 36.34 individuals (95% BCI 551-693) (Table 1). The density of the buffered study area was 1.09 ± 0.06 elk per km^2 (Figure 4). The *R-hat* values suggested MCMC convergence (< 1.1) for all model parameters.

The mean of the posterior of the scale detection parameter using the 9 km^2 grid was 2.04 ± 0.10 km (95% BCI 1.85-2.25), which was consistent with models using different grid sizes (1 km^2 = 2.07 ± 0.10 km; 4 km^2 = 1.99 ± 0.10 km), suggesting that grid resolution did not influence σ. Therefore, the model with a 9 km^2 grid was used for the remaining model for computational efficiency. The parameter estimates for the probability of detection function did not change dramatically between different buffer sizes, suggesting the model estimates were robust to changes in size of the state space (Table 1). The estimate for the covariate sex showed a slight increase in detection probability for females and the estimate for effort showed a slight increase in detection with increased effort.

Previous studies have shown a negative bias in models that do not relax the assumption of equal probability of detection at each trap when sampling from grouping species (López-Bao et al. 2018, Bischof et al. 2020). In this study, the model that did not

relax this assumption through a “trap”-level random effect produced a smaller population estimate of 512.94 ± 26.06 (95% BCI 464-567). This model also showed only a moderate fit with the individual encounter frequency goodness-of-fit test ($P = 0.678$), and a lack of fit with the trap-encounter frequency ($P = 0.000$). After adding the random effect, the estimate increased to 618 ± 36.34 individuals and the Bayesian *P*-values for the two goodness-of-fit tests were 0.478 and 0.478, respectively, suggesting an adequate model fit.

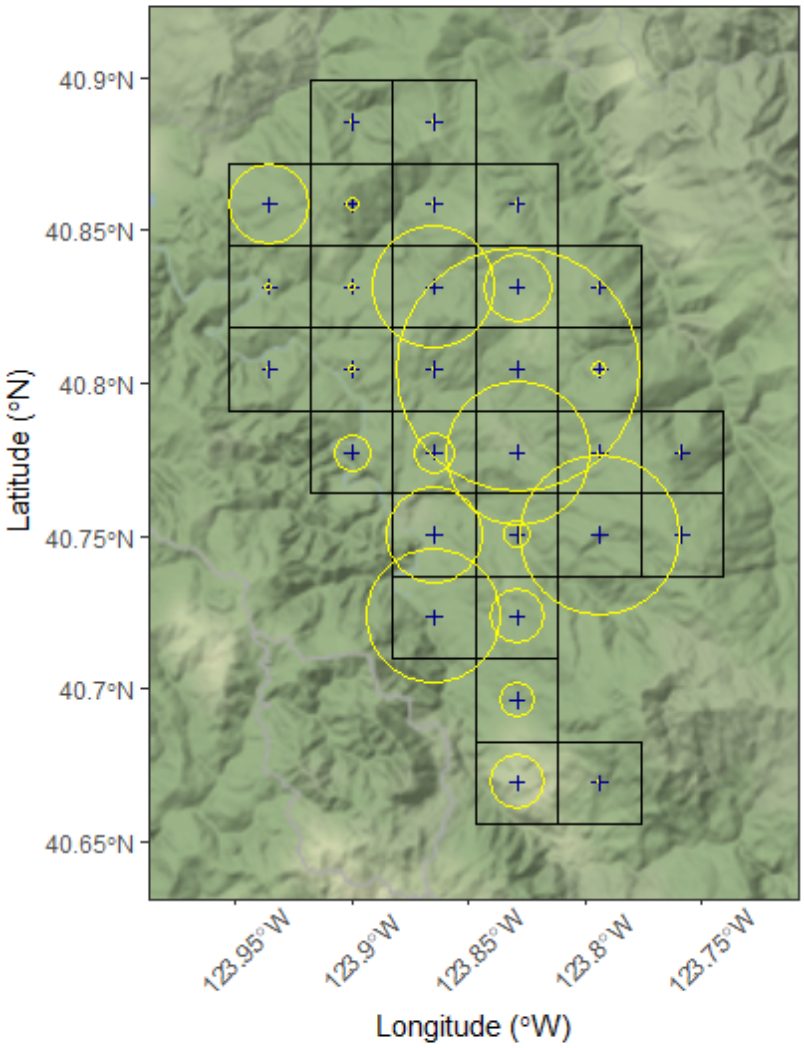

Figure 3. Map of area surveyed in January and February 2020 in Humboldt County, California, USA. A 9 km^2 grid is shown with spatial traps represented by blue "+", and the size of the yellow circles is proportional to the proportion of Roosevelt elk (*C. c. roosevelti*) 'captured' in that cell through fecal DNA.

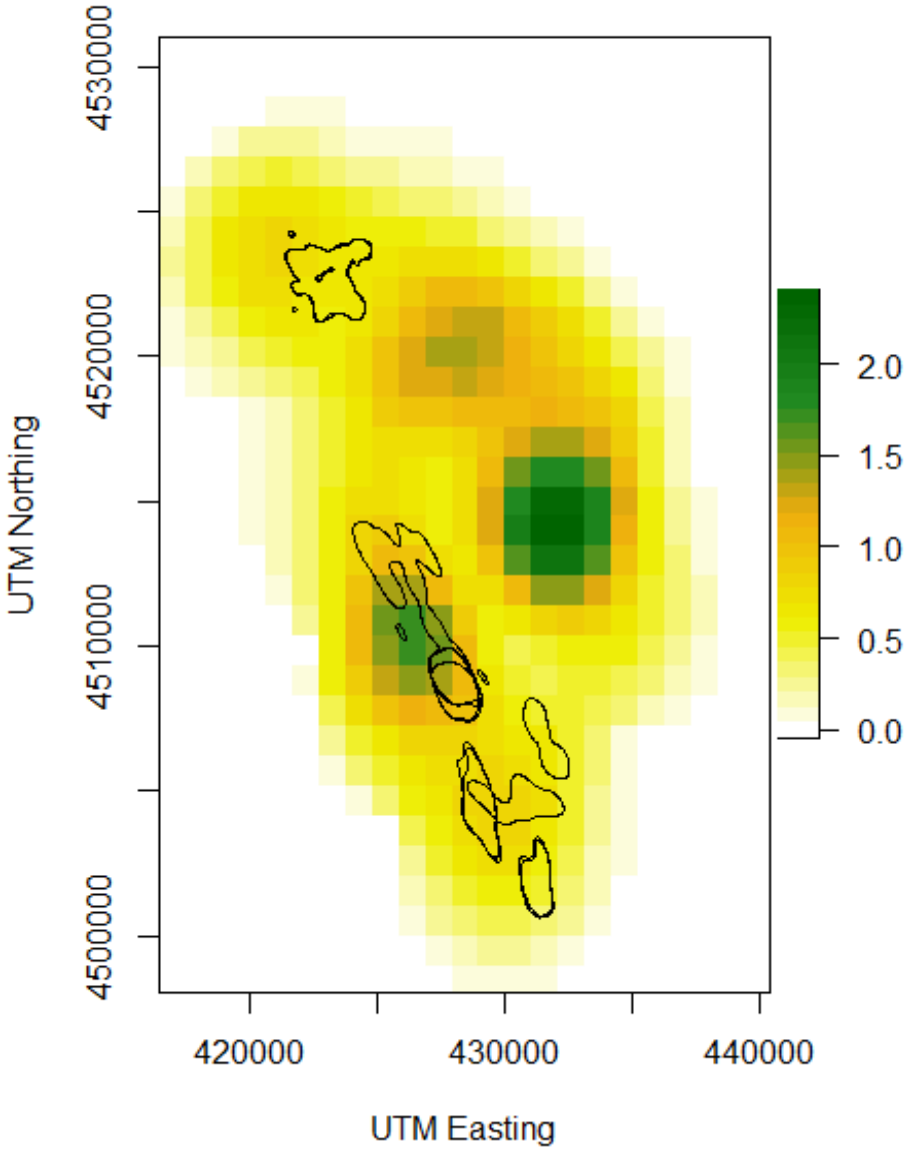

Figure 4. A density map of the posterior mean density of latent activity centers for genotyped Roosevelt elk (*C. c. roosevelti*) per km^2 in central Humboldt County, California, USA in January and February 2020. The 50% KDE with plug-in home ranges of the 6 collared cow elk are shown as black lines transposed over the density map. The high density area on the east side of the map suggests the presence of at least one group without a collared member.

Table 1. Posterior density estimates for Roosevelt elk (*C. c. roosevelti*) from a spatial capture-recapture model with a binomial point process with buffers of 4.5 km and 10 km. The estimated parameters are the covariates in the baseline encounter function: sex (β_1) and effort (β_2), scale detection parameter (σ), abundance (N), and density (D). All estimates are shown with ± standard deviation. Models used a logit detection function and were run for 50,000 iterations with a burn in of 25,000 and 3 chains for a total of 75,000 posterior samples.

	4.5 km	10 km
β_1	0.011 ± 0.01	0.018 ± 0.23
β_2	0.048 ± 0.04	0.043 ± 0.04
σ	2.04 ± 0.10	2.03 ± 0.10
N	618 ± 36.34	1294.05 ± 90.08
D	1.09 ± 0.06	1.12 ± 0.08

Cohesion and Home Range

A spatiotemporal analysis of select cow elk MCPs showed a wide range of daily overlap between elk pairs that varied by pair, month, and year (Figure 5). Present in both years, pair 1 had a mix of low, medium, and high overlap in 2019 (mean overlap = 42.9%), but showed a dramatically different pattern in 2020 when the cows had no overlapping MCPs in January, then overlap increased in February (mean overlap = 63.7%). Pair 2 had consistently high overlap (mean overlap = 82.6%) that decreased slightly over the 2020 study period. Conversely, pair 3 had consistently low overlap (mean overlap = 3.8%), with the amount of overlap increasing slightly from January to February in 2020. Due to the overall low overlap by pair 3, but roughly overlapping ranges for Pairs 1 and 3, I compared one cow from pair 1 to one cow from pair 3 for overlap during February 2020. These two cows exhibited high daily overlap for 42.3% of the MCPs with an average overlap of 65.6%.

The variability in overlapping home ranges is further demonstrated by the 25% and 50% KDE home ranges for these six collared cows (Figure 6). Pair 2 (not shown in Figure 6) represented a relatively distinct elk group with high cohesion and little overlap with any other collared individuals. Pair 1 (light and dark blue) and pair 3 (light and dark red) have almost entirely overlapping 25% KDEs, but the difference in their home ranges is more apparent when the 50% KDEs are compared. These KDEs suggests that the pairs may share parts of their core home range but have different movement and space use patterns on a larger scale. Pairs 1 and 3 were originally thought to belong to distinct elk

groups, but may instead represent a larger elk group with a range of cohesion levels between individual elk pairs through time.

The average home range size for the 7 collared cows in this study was 14.52 km^2 for the study period and 32.13 km^2 for the year. However, there was a wide range of sizes for the yearly home ranges with the smallest being 14.6 km^2 and the largest 93.9 km^2. The estimate for $\hat{\sigma}_{hr}$ was 1.59 km (study period) and 2.21 km for $\hat{\sigma}_{hr2}$ (full year); $\hat{\sigma}_{hr2}$ fell within the 95% Bayesian credible interval. Our estimated home range from the hra function was 78.32 km^2, which is large compared to the average yearly home range, but not unreasonable. This estimate was more similar to the yearly home range size derived from minimum convex polygons (MCP) with a mean of 65.10 km^2. Overall, these results suggest a relatively good biological performance of the model with a potentially slight overestimation of average space use.

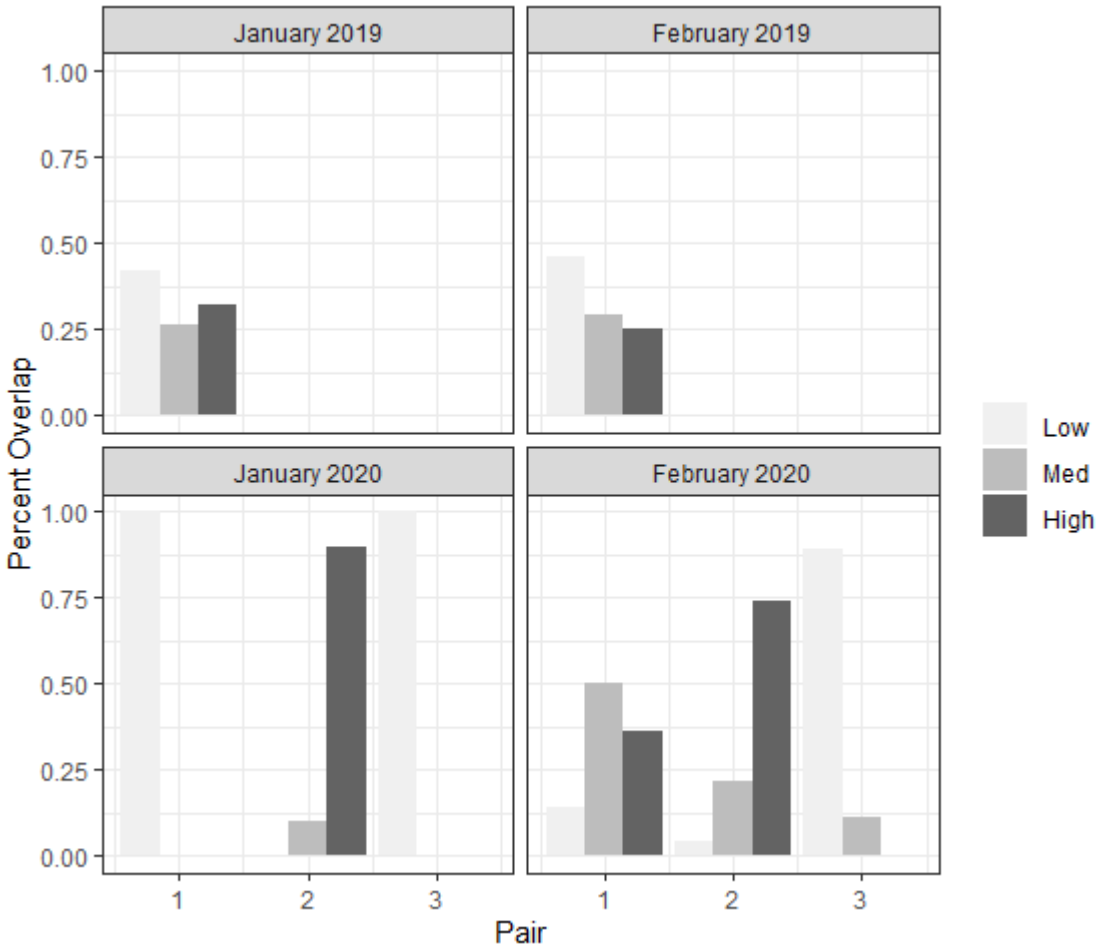

Figure 5. The proportion of overlapped minimum convex polygons (MCPs) that were within each percent overlap range: low (0-<25%), medium (>25-75%), high (>75-100%). The MCPs were created for each 24-hour period for three pairs of collared cow Roosevelt elk (*C. c. roosevelti*) in Jan and Feb of 2019 and 2020 in central Humboldt County, California, USA using the R package adehabitatHR v 0.4.18.

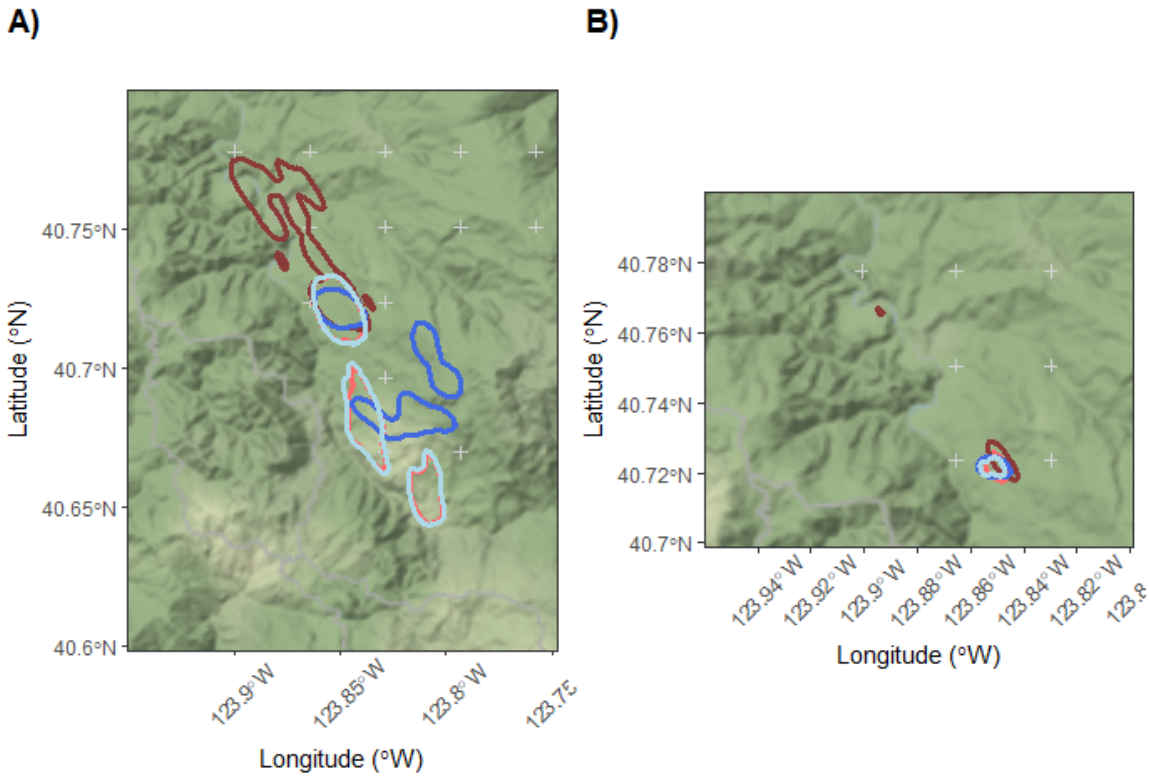

Figure 6. Kernel density estimate (KDE) with plug-in home ranges for Roosevelt elk (*C. c. roosevelti*) pair's 1 and 3 in Humboldt County, California, USA. The KDE home ranges only include points taken during the study period, January and February 2020. Each pair of elk from the same group are represented by the same color of different shades: pair 1 (light and dark blue) and pair 3 (light and dark red). Map A (left) shows the 50% KDE home ranges and map B (right) shows the 25% KDE home ranges.

DISCUSSION

Monitoring the Roosevelt elk population in central Humboldt County presents a unique challenge for wildlife managers. Previous work has shown the dense forest in Northern California makes traditional monitoring techniques ineffective (Weckerly and Kovacs 1998). This project used non-invasive genetic sampling combined with SCR modeling to obtain an abundance estimate of elk herds that were difficult to observe directly. Our density estimate of ~ 1 elk per km^2 was comparatively smaller than other estimates of Roosevelt and Tule elk in Northern California (Howell et al. 2002, Weckerly et al. 2004). However, elk populations throughout North America are notorious for dramatically different density estimates ranging from <1 elk per km^2 to estimates greater than 18 elk per km^2 (Stewart et al. 2009, Proffitt et al. 2015).

Our 2020 field methods allowed us to improve the count of male elk and the accuracy of the sex ratio estimate. However, the sex ratios from the fecal DNA included calves that are generally not included in sex ratio estimates used by wildlife managers. After removing the estimated average number of calves, the resulting sex ratio from the 2020 genotypes (100 females:34 males) was larger than the average sex ratio for the herds in Humboldt County (100 females: 19 males) from visual counts in 2021, suggesting that even repeated visual counts of some of the more highly visible herds may be undercounting bulls and yearling males. The adjusted ratio from 2019 genotypes produced a particularly low sex ratio, indicating targeted fecal sample collection of herds

using cow collar data may produce ratios with a strong bias against adult and yearling males.

The dramatic sex ratio differences in 2019 and 2020 may be due to some males, in particular yearlings, continuing to associate and move with cow-calf groups, and the unstructured search method enabled sampling from more groups, and therefore, more males. Likewise, by targeting the forested areas with the detection dog team, we further increased the number of unique male elk genotyped and increased recaptures of males, likely mature bulls, which were important for convergence of the SCR model parameter estimates (Furnas et al. 2018). We had similar recapture rates for both males and females and the baseline encounter probability parameter showed little difference in probability of detection between the sexes. This suggests that our field methods with SCR modeling were robust to the differences in distribution and behavior of males and females that can bias estimates from traditional monitoring methods.

The herding behavior of elk creates a unique challenge for SCR models with a homogeneous point process because it violates the assumption of independence between individual detections leading to overdispersed count data and negatively biased population estimates (Bischof et al. 2020). We believe this study minimized the bias from grouping behavior by relaxing the assumption of equal detection probability within each cell, and through spatially robust sampling with a high search effort.

Previous studies have shown that error in density estimates from SCR was reduced when all of the possible habitat was surveyed, and enough fecal pellets were successfully genotyped to result in sufficient unique individuals and spatial recaptures

(Brazeal and Sacks 2018, Bischof et al. 2020). In a study of an enclosed elk population of known size that followed similar field methods to this study, SCR predicted population estimates with relatively high precision and accuracy despite ignoring the grouping behavior of elk (Brazeal et al. 2018). Grouping should not be ignored in wild settings where elk have larger more heterogeneous home ranges than in limited free-range settings; however these studies collectively suggest that non-invasive genetic sampling with SCR can be a reliable method even with grouping species if search effort and spatial sampling is sufficiently high.

In our study area, we searched in targeted habitats across 30 cells, which encompassed ~80% of the study area. This spatially robust sampling with an unstructured survey design led to collecting from most, possibly all, the herds in the area. This potentially reduced the bias associated with grouping species and led to strong biological performance of the model. However, the model without the "trap"-level random effect still produced a much smaller estimate than the model with the random effect, this reflects a similar pattern found in previous work that demonstrated a slight negative bias with lower levels of grouping of less than 10 individuals (López-Bao et al. 2018). Therefore, relaxing the assumption of equal probability of detection within each cell potentially minimized the negative bias commonly associated with SCR and highly cohesive, grouping species.

Few SCR studies have looked at cohesion of movement among individuals and its impact on parameter estimates. This study presents one simple way to quantify cohesion among pairs in the same group, demonstrating that cohesion can vary considerably

between pairs and over time. The spatiotemporal analysis of cow elk MCPs indicated that some individuals in the same group moved semi-independently of each other while staying within the larger group home range. The elk pairs with high movement cohesion may have underlying bonds such as high genetic relatedness. Future studies could integrate relatedness into SCR modeling as a covariate to help explain why some individuals are 'captured' together more than others, which could be used to inform probability of detection or heterogeneity in density of activity centers. Similarly, it would be beneficial to measure cohesion and grouping within the SCR model itself, which will better measure the impact of those factors on SCR parameter estimates.

One of the benefits of SCR modeling is the use of spatial capture information on estimated home range centers and the scale detection parameter (Royle et al. 2013). The model's estimate of home range size was large compared to the home ranges from the collar data. However, it is important to be cautious when comparing these two different methods of estimating home range size. The method from Royle et al. (2013) assumed a circular home range that is independent from other individuals, neither of which is true for elk. These assumptions make this method more akin to the MCP home range method, which gave a more similar estimate. Conversely, the KDE method allowed for fragmented space use, which created more conservative home ranges. One of the other limitations of this comparison was the lack of GPS collar data for bull elk. We had little information on bull elk space use in this area, but when we compared σ for males and females in a SCR model, the estimates were within 0.1 km of each other suggesting similar home range sizes.

The latent activity centers from the model lined up well with the core home ranges of the collared elk groups during the study period. The high-density areas on the east side of the study area included at least one known group of elk with no collared individuals (Figure 4). Therefore, SCR analysis can be used to estimate the density of home range centers in the study area during the surveying time frame, which can be used to inform potential locations of human-wildlife conflict and predict home range locations of uncollared elk groups.

This study has demonstrated an efficient and reliable way to monitor elk populations where traditional methods such as aerial surveys are ineffective. Unstructured searches in high quality habitats captured more groups of elk and gave a more balanced sex ratio, circumventing the need to place collars on elk in remote areas to facilitate sampling. By combining the unstructured search method with an SCR model, this study obtained a reasonable estimate of the elk population size that can be used by wildlife management agencies to inform hunting quotas and future management plans.

MANAGEMENT IMPLICATIONS

The unstructured search method used in this study was an efficient and effective way to survey large areas for a species with high heterogeneity in density and distribution. It also reduced the need to spend time delineating transects in the field and allowed for the flexibility to change course when areas of high use by elk were found. This study showed that an unstructured search method, in combination with the use of a detection dog, can help to increase the count of bull elk who may have different spatiotemporal habitat use patterns than the cow-calf groups.

We chose to sample in the winter months to avoid immigration during rut in the fall and emigration during parturition in the spring. The mild climate in Humboldt County leads to high survival of adult elk, and by starting surveys in January, we avoided the first 14 weeks after most parturition events when calf mortality is highest (Nigon 2020). Winter was also a beneficial time to sample due to decreased space use by elk, which increased the chances of capturing samples from the greatest number of unique individuals. On the other hand, winter months can be a hindrance to successful sampling due to increased precipitation, especially in the Pacific Northwest, which can wash off fecal DNA and reduce genotyping success from fecal pellets (Brinkman et al. 2010). There was a decline in the genotyping success rate between 2019 and 2020, which is likely due to the targeted sampling of recent collared elk locations in 2019 increasing the proportion of fresh samples collected. This may indicate that more samples will be needed using the unstructured method to obtain a similar number of captures and

recaptures as the targeted sampling. Overall, this study avoided sampling on days of rain and maintained a relatively high genotyping success rate in 2019 and 2020, which was found in a similar study that also sampled during the winter months (Mena 2019). Therefore, the benefits from sampling during the rainy season greatly outweighed the negative impacts of inclement weather.

We recommend keeping the study area small enough that the majority of suitable habitat can be surveyed. This is important to increase the probability of sampling from all elk groups in the area and reduce the bias associated with grouping behavior. Targeting both open grassy habitat and forested habitat was also important for increasing unique genotypes and recaptures. However, there were fewer than expected unique individuals found only in the forest, suggesting an equal search effort in both forest and open habitat may not be necessary. We recommend focusing efforts on the open grassy areas of high habitat suitability, and adding forested habitat if concerted effort is made to focus on bull elk in the region.

Lastly, the overdispersion in the count data from grouping behavior cannot be overlooked. This study found that relaxing the assumption of equal probability of detection within each cell increased goodness-of-fit and reduced the negative bias incurred from grouping behavior. However, some bias from the dependent nature of elk movement likely still impacts the results and further research is needed to better account for the highly social behavior of Roosevelt elk.

LITERATURE CITED

Barker, R. J., M. R. Schofield, W. A. Link, and R. John. 2017. On the reliabiity of N-mixture models for count data. Biometrics 74:23–24.

Bischof, R., P. Dupont, C. Milleret, J. Chipperfield, and J. A. Royle. 2020. Consequences of ignoring group association in spatial capture–recapture analysis. Wildlife Biology 2020:1–10.

Bliss, L. M., and F. W. Weckerly. 2016. Habitat use by male and female Roosevelt elk in northwestern California. California Fish and Game 102:8–16.

Brazeal, J. L., and B. N. Sacks. 2018. Use of an enclosed elk population to assess two non- invasive methods for estimating population size.

Brinkman, T. J., M. K. Schwartz, D. K. Person, K. L. Pilgrim, and K. J. Hundertmark. 2010. Effects of time and rainfall on PCR success using DNA extracted from deer fecal pellets. Conservation Genetics 11:1547–1552.

Calenge, C. 2006. The package adehabitat for the R software: tool for the analysis of space and habitat use by animals. Ecological Modelling 197:1035.

California Departement of Fish and Wildlife. 2018. Elk conservation and management plan.

Dahlgren, D. K., R. Dwayne Elmore, D. A. Smith, A. Hurt, E. B. Arnett, and J. W. Connelly. 2012. Use of dogs in wildlife management. Pages 140–153 *in*. Wildlife Techniques Manual. Seventh edition. The Wildlife Society Inc., Washington, D.C.

Donovan, G., and P. Champ. 2009. The Economic Benefits of Elk Viewing at the Jewell

Meadows Wildlife Area in Oregon. Human Dimensions of Wildlife 14:51–60.

Franklin, W. L., A. S. Mossman, and M. Dole. 1975. Social organization and home range of Roosevelt elk. Journal of Mammalogy 56:102–118.

Furnas, B. J., R. H. Landers, S. Hill, S. S. Itoga, and B. N. Sacks. 2018. Integrated modeling to estimate population size and composition of mule deer. The Journal of Wildlife Management 82:1429–1441.

Gelman, A., J. Carlin, H. Stern, D. Dunson, A. Vehtari, and D. Rubin. 2014. Bayesian Data Analysis. 3rd edition. Taylor & Francis.

Gibbs, J. P. 2000. Research techniques in animal ecology. Columbia University Press, New York.

Goode, M. J., J. T. Beaver, L. I. Muller, J. D. Clark, F. T. van Manen, C. A. Harper, and P. S. Basinger. 2014. Capture-recapture of white-tailed deer using DNA from fecal pellet groups. Wildlife Biology 20:270–278.

Google Earth. 2018. <https://www.google.com/earth/>. Accessed 24 Apr 2019.

Griffin, P. C., B. C. Lubow, K. J. Jenkins, D. J. Vales, B. J. Moeller, M. Reid, P. J. Happe, S. M. Mccorquodale, M. J. Tirhi, J. P. Schaberl, and K. Beirne. 2013. A hybrid double-observer sightability model for aerial surveys. The Journal of Wildlife Management 77:1532–1544.

Harris, R. B., J. Winnie, S. J. Amish, A. Beja-Pereira, R. Godinho, V. Costa, and G. Luikart. 2010. Argali abundance in the Afghan Pamir using capture–recapture modeling from fecal DNA. Journal of Wildlife Management 74:668–677.

Humboldt County General Plan Update: Natural Resources and Hazards. 2002. Eureka.

Kellner, K. 2019. jagsUI: A Wrapper Around “rjags” to Streamline “JAGS” Analyses. <https://cran.r-project.org/package=jagsUI>.

Kohn, M. H., E. C. York, D. A. Kamradt, G. Haught, R. M. Sauvajot, and R. K. Wayne. 1999. Estimating population size by genotyping faeces. Proceedings of the Royal Society of London. Series B: Biological Sciences 266:657–663.

Kolbe, N. R., and F. W. Weckerly. 2015. Home-range overlap of Roosevelt elk herds in the Bald Hills of Redwood National Park. California Fish and Game 101:208–217.

López-Bao, J. V., R. Godinho, C. Pacheco, F. J. Lema, E. García, L. Llaneza, V. Palacios, and J. Jiménez. 2018. Toward reliable population estimates of wolves by combining spatial capture-recapture models and non-invasive DNA monitoring. Scientific Reports 8:1–8.

Lounsberry, Z. T., T. D. Forrester, M. T. Olegario, J. L. Brazeal, H. U. Wittmer, and B. N. Sacks. 2015. Estimating sex-specific abundance in fawning areas of a high-density Columbian black-tailed deer population using fecal DNA. Journal of Wildlife Management 79:39–49.

Lubow, B. C., and J. I. Ransom. 2016. Practical bias correction in aerial surveys of large mammals: Validation of hybrid double-observer with sightability method against known abundance of feral horse (*Equus caballus*) populations. PLoS ONE 11:1–15.

Lukacs, P. M., and K. P. Burnham. 2005. Review of capture-recapture methods applicable to noninvasive genetic sampling. Molecular Ecology 14:3909–3919.

Månsson, J., H. Andrén, and H. Sand. 2011. Can pellet counts be used to accurately describe winter habitat selection by moose *Alces alces*? European Journal of

Wildlife Research 57:1017–1023.

McCorquodale, S. M. 2001. Sex-Specific Bias in Helicopter Surveys of Elk: Sightability and Dispersion Effects. The Journal of Wildlife Management 65:216.

Mena, R. 2019. Targeting social cohesion in female roosevelt elk (*Cervus canadensis roosevelti*) groups minimizes survey efforts for fecal dna capture-recapture estimates of abundance. HSU thesis and projects. Humboldt State University.

Moeller, A. K., P. M. Lukacs, and J. S. Horne. 2018. Three novel methods to estimate abundance of unmarked animals using remote cameras. Ecosphere 9:1–15.

Mohr, A. 2020. A tale of two cervids: habitat selection and spatial ecology of Roosevelt and tule elk in California. HSU theses and projects. Humboldt State University.

Nigon, E. 2020. Estimates of calf survival and factors influencing Roosevelt elk mortality in northwestern California. HSU theses and projects. Humboldt State University.

Palsbøll, P. J., J. Allen, M. Bérube´, P. J. Clapham, T. P. Feddersen, P. S. Hammond, R. R. Hudson, H. Jørgensen, S. Katona, A. H. Larsen, F. Larsen, J. Lien, D. K. Mattila, J. Sigurjónsson, R. Sears, T. Smith, R. Sponer, P. Stevick, and N. Øien. 1997. Genetic tagging of humpback whales. Nature 388:767–769.

Poole, K. G., D. M. Reynolds, G. Mowat, and D. Paetkau. 2011. Estimating mountain goat abundance using DNA from fecal pellets. Journal of Wildlife Management 75:1527–1534.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org/>.

Reed, S. E., A. L. Bidlack, and W. M. Getz. 2011. Detection distance and environmental factors in conservation detection dog surveys. Journal of Wildlife Management 75:243–251.

Rowcliffe, J. M., J. Field, S. T. Turvey, and C. Carbone. 2008. Estimating Animal Density Using Camera Traps without the Need for Individual Recognition. Journal of Applied Ecology 45:1228–1236.

Royle, J. A., R. B. Chandler, R. Sollmann, and B. Gardner. 2013. Spatial Capture-Recapture: First Edition. Academic Press. Elsevier Inc.

Sacks, B. N., Z. T. Lounsberry, T. Kalani, E. P. Meredith, and C. Langner. 2016. Development and characterization of 15 polymorphic dinucleotide microsatellite markers for tule elk using hiseq3000. Journal of Heredity 107:666–669.

Sugihara, N. G., L. J. Reed, and J. M. Lenihan. 1987. Vegetation of the bald hills oak woodlands, Redwood National Park, California. Madroño 34:193–208.

Walter, W. D., and J. W. Fischer. 2016. Manual of Applied Spatial Ecology.

Walter, W. D., J. W. Fischer, S. Baruch-Mordo, and K. C. Vercauteren. 2011. What Is the Proper Method to Delineate Home Range of an Animal Using Today's Advanced GPS Telemetry Systems: The Initial Step. Modern Telemetry 249–268.

Weckerly, F., K. McFarland, M. Ricca, and K. Meyer. 2004. Roosevelt elk density and social segregation: foraging behavior and females avoiding larger groups of males. The American Midland Naturalist 152:386–399.

Weckerly, F. W., and K. E. Kovacs. 1998. Use of military helicopters to survey an elk population in North Coastal California. California Fish and Game. Volume 84.

Woodruff, S. P., P. M. Lukacs, D. Christianson, and L. P. Waits. 2016. Estimating Sonoran pronghorn abundance and survival with fecal DNA and capture-recapture methods. Conservation biology : the journal of the Society for Conservation Biology 30:1102–1111.

Woods, J. G., D. Paetkau, D. Lewis, B. N. Mclellan, M. Proctor, and C. Strobeck. 1999. Genetic tagging of free-ranging black and brown bears. Wildlife Society Bulletin 27:616–627.

APPENDIX

The quality of habitat in each cell was calculated based on a habitat suitability model developed for elk in this region (Mohr 2020), and the range of suitability values within each grid cell was compared to the frequency those values were used by 19 collared cows in Humboldt County and 14 collared cows in Del Norte County. Based on the distribution of GPS points, habitat values less than the 1% quantile (-2.094) were considered unsuitable habitat, values between -2.094 and 0.317 were considered low habitat suitability, and values 0.317 or greater were considered high habitat suitability (Figure A1). Cells were unavailable for surveying if more than 25% of their area was unsuitable habitat, or less than 5% of the area was classified as high habitat suitability.

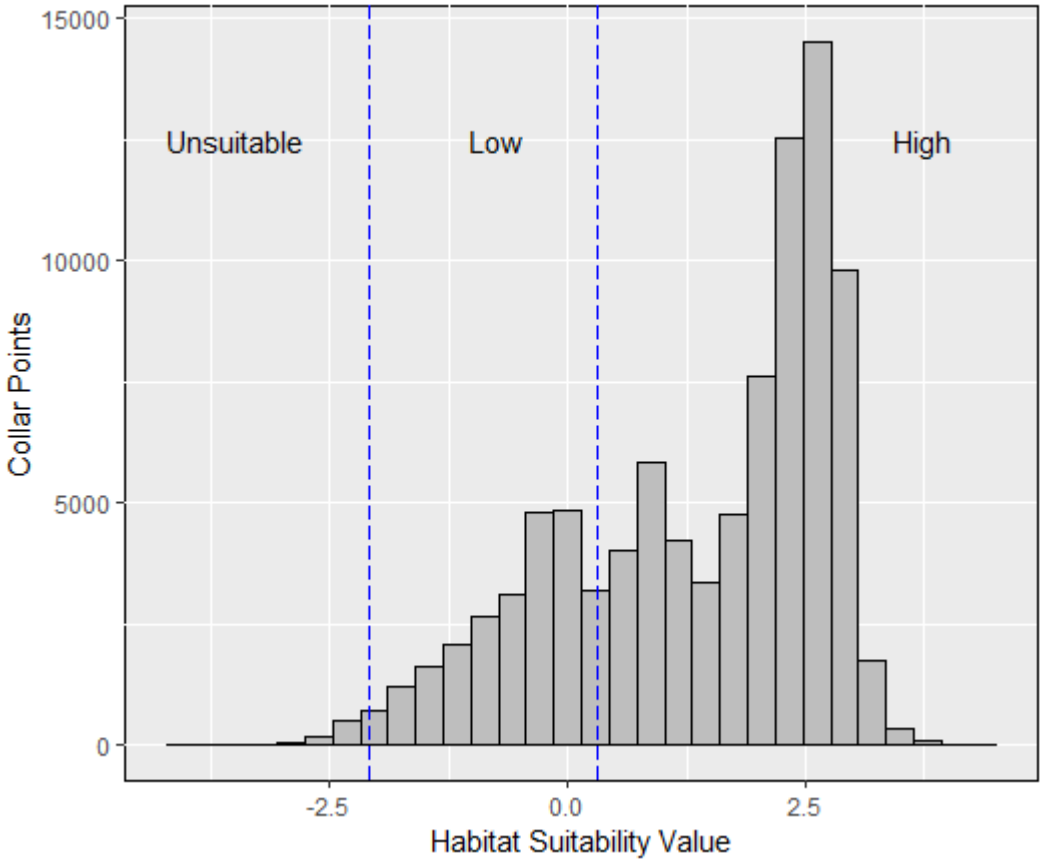

Figure A1. Distribution of habitat suitability values at GPS points from all collared cows (n = 33) in Humboldt and Del Norte counties, California, USA from 2018 to 2020. The blue dash represents the bottom 1% of points (x = -2.094) and the 25% quantile (x = 0.317).